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Phylogeny of the Arionidae and other pulmonates based on the terminal genital ducts (Mollusca)

by

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ABSTRACT

The ontogeny and anatomy of the genus *Arion* is compared with that of species belonging to other subfamilies of Arionidae. It is suggested that the striking differences between the genital system of the Arioninae and that of the other subfamilies are merely due to deviations from the basic ontogeny.

The relationship between the pulmonate subfamily Arioninae and other subfamilies of Arionidae is problematic due to striking differences in the genital anatomy. A comparative study of the ontogeny, and the resulting anatomy of these groups, however, seems to indicate a common ancestor.

The genital aperture of the ancestral pulmonate was situated close to the pneumostome. I (Sirgel, in press) have argued that this aperture disappeared and that the system acquired a new aperture by opening slightly more anteriorly into the posterior end of a superficial groove which developed on the right side of the body (Fig. 1).

I believe that during the evolution of Stylommatophora this groove gradually closed from its posterior towards its anterior end, to become a duct, thus displacing the genital aperture anteriorly towards the base of the right tentacle.

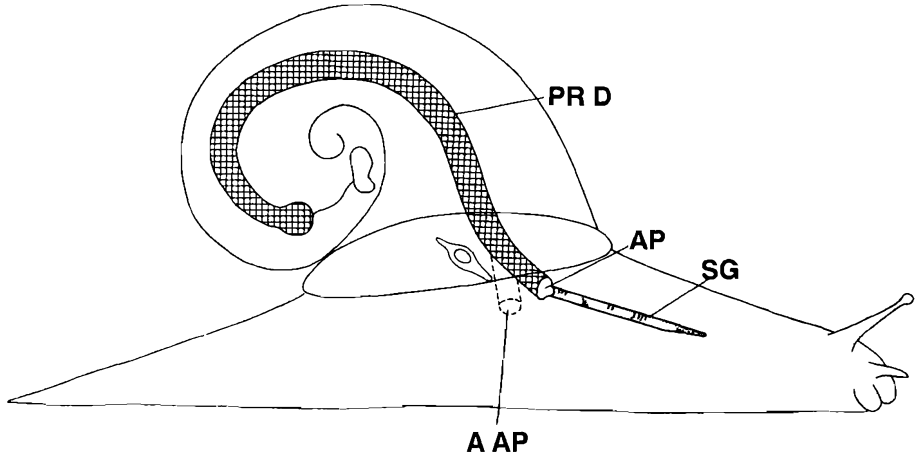

Fig. 1. Diagram to show the disappearance of the ancestral genital aperture and the acquisition of a new aperture opening into a superficial groove. A AP = position of ancestral aperture, AP = genital aperture, PR D = primary genital duct, SG = superficial groove.

Furthermore this added duct divided longitudinally into two, one becoming the free oviduct and vagina, and the other the proximal part of the vas deferens (Fig. 2).

Concomitantly with this development, an invagination of the body wall, near the base of the right tentacle, developed into another element of the genital system, the primary penis. This longitudinally split off a slender duct which later became the distal part of the Stylommatophoran vas deferens (Fig. 2).

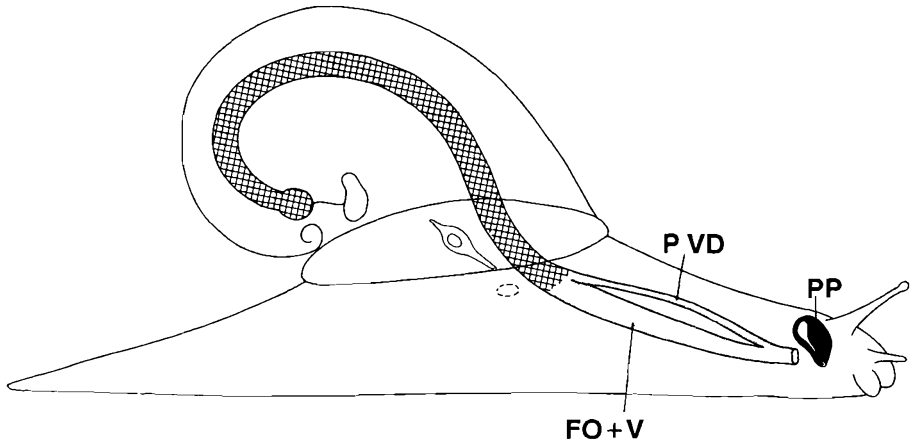

Fig. 2. Diagram to show a more advanced stage in the phylogenetic displacement of the genital aperture towards the tentacles. FO + V = free oviduct & vagina, PP = primary penis, P VD = proximal vas deferens.

Eventually the aperture of the genital system was displaced so far anteriorly that it became situated close to that of the primary penis. A continued invagination of the body wall surrounding both these apertures led to the addition of a common genital atrium to the system (Fig. 3). It also enabled the proximal vas deferens to connect to the distal section derived from the penis. I agree with Simroth (1928) that the genital atrium distally adds sections to either the vagina or penis through secondary evaginations in the direction of one or the other of these structures (Fig. 3).

These suggestions on the phylogenetic development are supported by the ontogeny of the arionid subfamily Ariopeltinae and they seemingly can account for the conditions found in all the subfamilies of Arionidae and other Stylommatophora with anteriorly situated genital apertures. The subfamily Arioninae, and more specifically the genus *Arion*, however, differs from these subfamilies in: 1. The genital aperture being situated much further posteriorly in the vicinity of the ancestral position. 2. By the epiphallus opening directly into a large bipartite genital atrium without the intervention of a penis (Fig. 4A). 3. By the lack of a vagina; having only a short free oviduct. 4. By the spermathecal duct opening directly into the genital atrium.

At first sight this seems to indicate that the ancestral genital aperture has been maintained and that no superficial groove developed in this group. This view

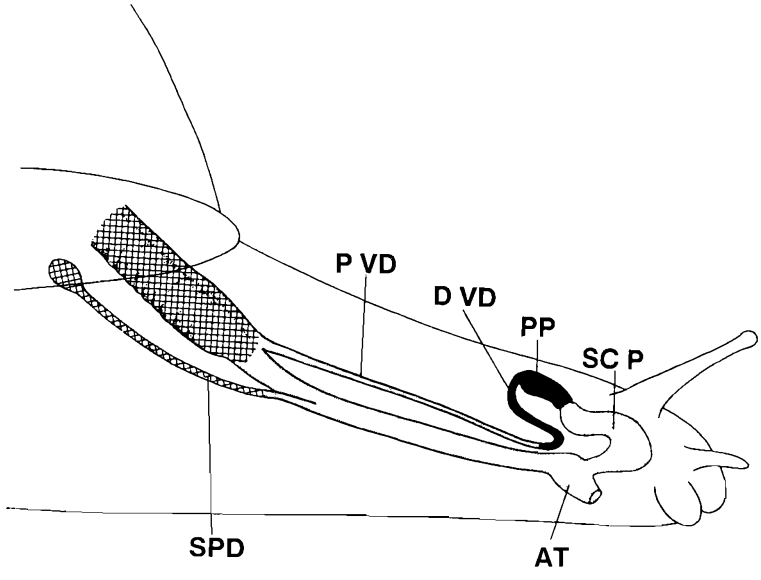

Fig. 3. Diagram of genital system after the development of the genital atrium. AT = genital atrium, D VD = distal vas deferens, PP = primary penis, P VD = proximal vas deferens, SC P = secondary added part of penis, SPD = spermathecal duct.

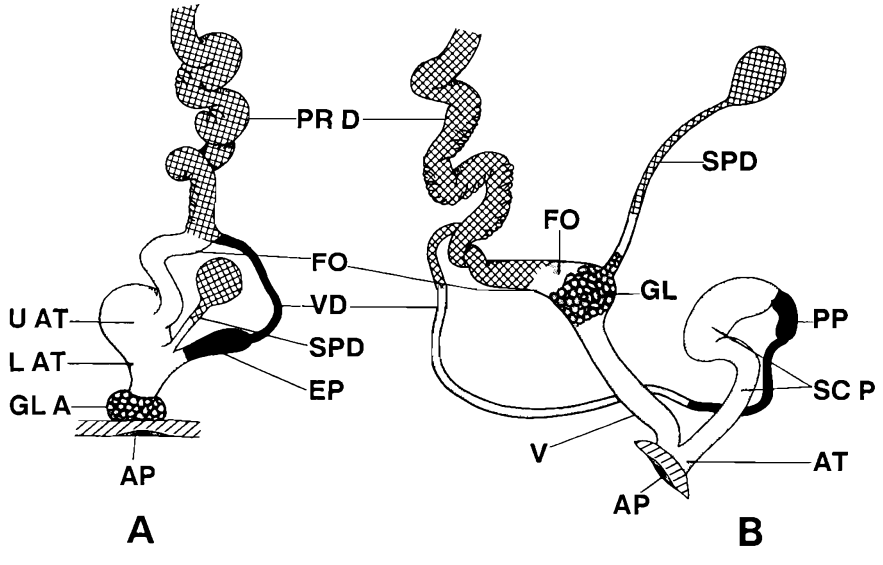

Fig. 4. A. Diagram of the distal parts of the genital system of *Arion*. B. Distal parts of the genital system of *Ariopelta* representing the basic type of system found in many pulmonates with an anteriorly situated genital aperture. AP = genital aperature, AT = genital atrium, EP = epiphallus, FD = free oviduct, GL = glandular portion resembling lower atrium of *Arion*, GL A = glandular portion of lower atrium, L AT = lower genital atrium, PP = primary penis, P RD = primary genital duct, SCP = secondary added part of penis, SPD = spermathecal duct, U AT = upper genital atrium, V = vagina, VD = vas deferens.

seems to be supported by the fact that several authors (Pabst 1914, Hoffmann 1922 & 1925, Hochpöchler 1979, Nel 1984) describe the epiphallus as developing directly from the wall of an atrium, which they consider to be part of the primary genital duct. If so, this would deviate so fundamentally from the phylogeny here suggested for the other subfamilies of Arionidae that it should exclude them as close relatives of Arioninae. A closer consideration, however, indicates that all these groups underwent the same basic evolutionary process including the development of a superficial groove and its closure to become a duct.

I now suggest that the striking differences between the arionine genital system and that of the other subfamilies are merely due to the arionine superficial groove closing from its anterior towards its posterior end during ontogeny. This would displace the anterior genital aperture towards the posterior end of the groove while adding a duct, homologous to the free oviduct, vagina and proximal vas deferens of the other subfamilies, distally to the atrium as a lower atrium (Fig. 5). The anlage of the primary penis would thus be carried deep into the body on the original atrium which still develops from the anterior end of the groove.

It is also suggested that, as in the other subfamilies, the ancestral genital aperture disappears during ontogeny while the resulting blind end of the primary duct is thought to grow slightly anteriorly in its search for a new aperture (Figs 5B, C, D). It is further suggested that instead of opening into the posterior end of the superficial groove in this case it joins the upper atrium (original atrium), thus gaining an indirect passage to the exterior.

One of the these deviations from the basic ontogeny could induce the others, resulting in the drastically different-looking end product. One such an induction could be that the development of the primary penis is retarded to such an extent that it is only discernible after the primary genital duct has joined the genital atrium (Fig. 5D). This would explain why Pabst (1914) and others describe the epiphallus, which I believe to represent the primary penis, as developing from a genital atrium which they consider part of the primary genital system instead of originating from an independent extrapallial anlage as depicted in Fig. 5A.

I suggest that the longitudinal separation of the spermathecal duct from the distal part of the primary gonoduct is extended anteriorly beyond the primary gonoduct in all these groups. This would displace its junction with the rest of the system onto the genital atrium in Arioninae (Figs 5C, D, E). Similarly it is suggested that a part of the upper genital atrium evaginates or splits off, thus adding a short free oviduct distally to the primary gonoduct. These suggestions would account for: 1. More posteriorly situated genital aperture (Fig. 5E) 2. Absence of the vagina (Fig 4 & 5). 3. Short free oviduct. 4. Opening of the spermathecal duct into a large bipartite genital atrium. 5. The absence of a penis is also explained by the epiphallus representing the primary penis while the larger secondary added sections of the penis in other groups (Fig. 4B) is here represented by a part of the upper atrium (Fig. 4A). In this respect it may be noted that Pabst (1914) did mention the possibility that the upper atrium of *Arion* could possibily represent the penis. The addition of the duct, which in the other subfamilies forms the oviduct, vagina and proximal part of the vas deferens, to the distal end of the system as the lower atrium (Fig. 4A) also explains Pabst's (1914) observation that

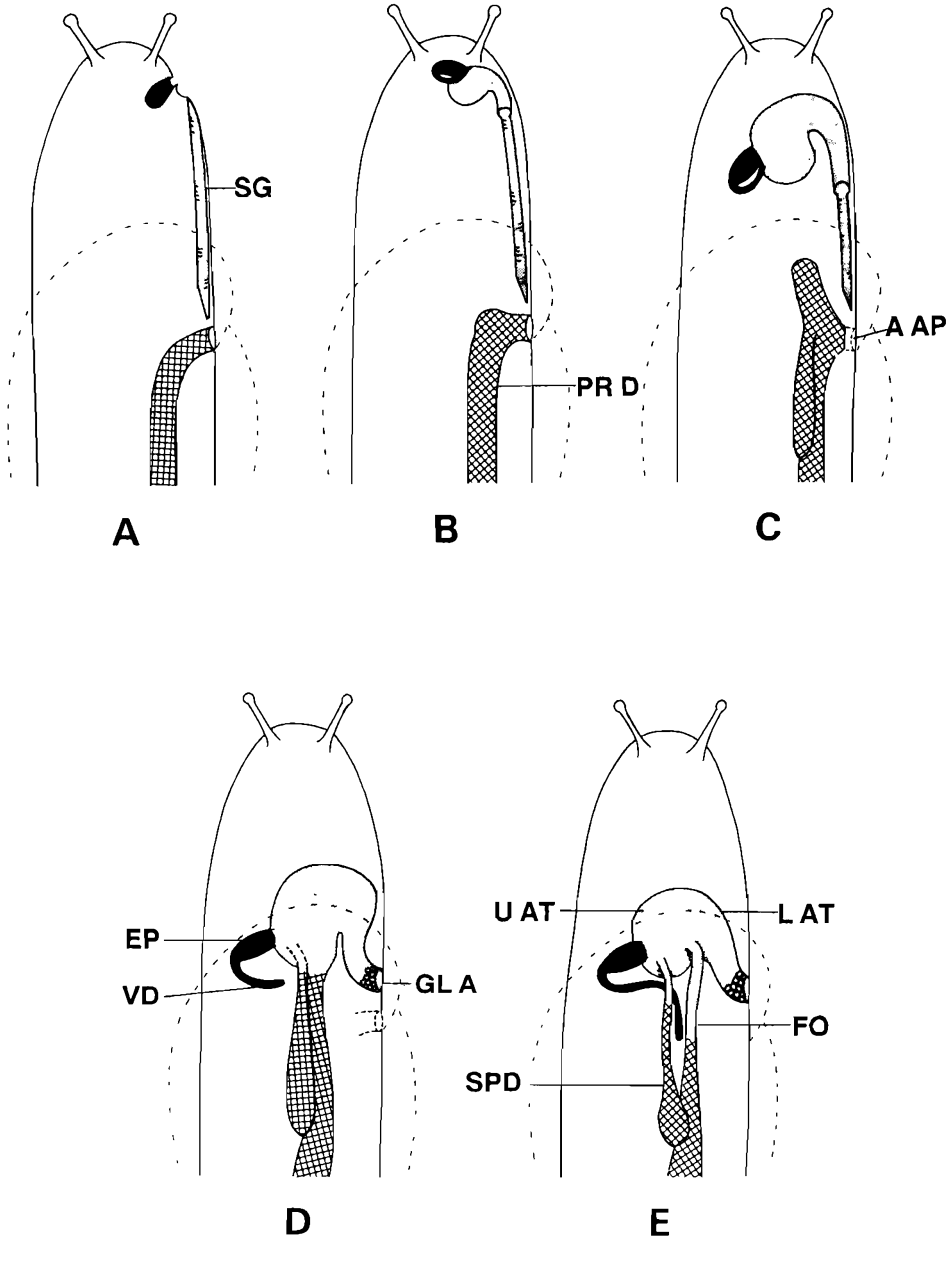

Fig. 5. Diagrams to illustrate the suggested evolution of the distal parts of the genital system in *Arion*. A AP = position of ancestral aperture, EP = epiphallus (= primary penis); FO = free oviduct, GL A = grandular portion of lower atrium, L AT = lower atrium, PRD = primary duct, SPD = spermathecal duct SG = superficial groove, U AT = upper atrium, VD = vas deferens.

the vas deferens, during the ontogeny of *Arion*, develops from only one centre, the epiphallus (thus the primary penis), from where it grows towards the sperm-oviduct (Figs 5C D E). This illustrates that only the distal vas deferens develops in *Arion* (Fig. 4A).

Further support for the suggestion that the homologue of the free oviduct and vagina of the other subfamilies is added distally to the atrium in *Arion*, is found in the fact that the wall of the most distal portion of the atrium in *Arion* consists of large glandular cells (Fig. 4A) similar to those found proximally to the atrium in the free oviduct/vagina complex of many other Stylommatophora (Fig. 4B) with an anteriorly situated genital aperture. It should be noted that similar looking cells are also found in the body wall of these molluscs particularly in the vicinity of and on the edge of the mantle. This, incidentally, is the area from which the lower part of the atrium of *Arion* and its suggested homologue, the free oviduct/vagina complex of the other subfamilies, is suggested to develop.

The genital systems of the arionine genera *Geomalacus* and *Letourneuxia* can seemingly also be explained in accordance with the suggestions made here. They, however, will be discussed in a future paper.

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